

NOTES ON THE POLLINATION OF SOME SOUTH AFRICAN CYCADS.

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The following notes on the pollination of the Cycads which grow within easy reach of East London are the result of observations made during the last seven or eight years, sometimes sporadically, sometimes systematically.

I have been able for a time to keep over a dozen cones of *Stangeria* under continuous observation during the critical period and verify my former conclusions.

The notes contain little that is new; by far the most important link in the chain of evidence for the insect pollination of *Encephalartos villosus* was discovered by Miss Pegler and recorded by Professor Pearson in 1906 (*Transactions* of the South African Philosophical Society, vol. xvi., part 4), while my general conclusions are largely those foreshadowed by the latter at the same date.

ENCEPHALARTOS ALTENSTEINII, Lehm.

It is hard to say what is the natural habitat of this species. Along the deep valleys eroded by our rivers and streams it is found now clinging precariously to the face or crowning the top of some precipitous krantz now hidden amid the shrubs and trees of a wooded ravine. Seldom or never does it leave the river valley for the open grass formation of the surrounding country. From its relatively greater frequency—at times it is almost social—in exposed situations and the almost complete absence of cone production in the woodland forms, I am disposed to regard it as a sun rather than a shade plant. In the open form cones are produced in fair abundance, there being few years in which some cannot be obtained, but a considerable variation exists in regard to the time at which they make their appearance. I have found them just emerging as early as the middle of November and as

late as the first week of February of the following year. In the great majority, however, the cones are visible in the last week of December. Coning is heralded by a flattening out of the apex of the trunk and the gradual depression of the leaves from a semi-erect to a horizontal position, so that the full-grown cones come to occupy a comparatively conspicuous position—a point which may be regarded as equally favouring anemophily by exposing the cones to the full benefit of the wind, or entomophily, in the same manner as the entomophilous angiosperm does not conceal its attractive blossom among its leaves.

Staminate cones are somewhat more abundant than ovulate ones; not so much, however, because the number of male plants is greater than that of the female as because more of the former are produced on an individual stem. Female cones are usually borne in ones, twos, or threes, rarely more, while the males are produced in threes, fours, or fives, or even sevens, rarely ones or twos. There is also some evidence that male plants cone more frequently than females, although the number of specimens under observation would require to be sufficiently great to eliminate individual eccentricities before one could be certain.

The male cones mature and the microsporangia begin to dehisce about the second week of April on an average, but pollen continues to be shed for two weeks or longer. At this date the male cone is about 20 inches high, inclusive of the short peduncle. The sporophylls are widely separated, so that there is free play for the wind or the entrance of insect visitors. When ripe the cone is of a pale brown colour, and is a conspicuous object in contrast with the dull green of the leaves—a contrast which is intensified as the freshly shed pollen dusts all parts with a coating of white. A faint but distinct odour is emitted which is not unpleasant, yet with one exception I have observed few insect visitors until decomposition has begun. The single exception is formed by a species of curculionid beetles, which have been referred to the genus *Phlæophagus*. The most abundant species has a much-depressed body of dark shining brown colour, and the female is furnished with a long rostrum. In April, 1908, a single male cone, one of three which I collected and brought home wrapped in paper, yielded 437 individuals, and several escaped during the removal of the cone. Since that date I have again and again found these weevils in great abundance on the cones at the time the pollen is ripe. Their bodies are inevitably buried in pollen, and masses adhere to the base of the rostrum and to the legs.

In the specimens which I brought home in 1908 I found that the pollen was still adhering to their bodies three days after they were removed from the cone, although during that time they had had the free run of the room. Although I had known these weevils for some years previously, and knew that they possessed functional wings, I had

never actually seen them flying, although at times there must have been dozens of them crawling all over the room in which I worked. As the point seemed of some importance, I tried dropping them suddenly from a height off the blade of a knife. After many hours of this diverting occupation I at last succeeded in making two or three spread their wings and entrust themselves to the air. (Need I add that the very next evening many of them flew round and round the room *sua sponte*.)

Two points were then established—that *Phlæophagus* could make a flight of some yards, and that pollen could adhere to its body for at least 60 hours.

At the time of pollination the female cone is 14 inches high with no visible peduncle. The colouring is an indefinite green with a suspicion of yellow, and could not be described as conspicuous. Nor is there any perceptible odour. Although I have examined over a score of female cones during the time the pollen is being shed and have had three under daily observation in my own garden I have never noted any separation of the sporophylls. Although I still feel bound to believe that it must occur, yet it must be only to a very limited extent—a condition which, while not altogether excluding anemophily in this species, certainly renders it much less probable; for the exposed parts of the sporophylls stand almost horizontally and do not overlap, so that unless the separation were very marked only wind-borne pollen coming horizontally could effect an entrance, and only those ovules on the side of the prevailing winds would be fertilised. But in all the cones which I have worked through, even from plants growing on the outside of a group, embryos had been formed in uniform proportions on all sides.

Long before I was aware that *Phlæophagus* visited the staminate cones of *E. Altensteinii* I knew that it was hardly possible to find a mature ovulate cone in which a large percentage of the ovules were not parasitised by the same insect, but was wholly unaware when the eggs were deposited. Miss Pegler's observations on *E. villosus*, recorded by Professor Pearson, suggested a line of inquiry when once I had proof that the male cones of *E. Altensteinii* were also visited by these weevils.

A visit paid on the third day to the two remaining male cones—found in April—showed that although there was still some fresh pollen the weevils had disappeared. Some thirty paces lower down the valley there was a female plant with two cones. An external examination of these revealed no sign of any insect, and as the sporophylls showed no sign of separation I concluded that wherever the insects had gone it was not to these. I was therefore much surprised, on cutting open one of the cones, to find scores of weevils present. Once past the barrier formed by the peltate portion of the sporophylls it was easy to see that their movements were comparatively unrestricted, especially near the cone axis. A lens examination

showed traces of what might be pollen, and its presence was confirmed later by the microscope, when eleven out of twenty examined had pollen still adhering to their bodies. Unfortunately the figures are not of much value, as for several hours all the weevils were packed together in the same test tube and it is possible that a transference of pollen may have taken place.

I have since then found two other ovulate cones with pollen-bearing weevils.

In trying to work out the life-history of this interesting insect, I have found that the development from egg to adult coincides exactly with the period that elapses between the pollination and the disintegration of the female cone of *E. Altensteinii*. In ovules up to three months old one can find no trace of the insect at any stage of its development, while from June onwards they are easy to find. The life-history appears to be as follows: The eggs up to a dozen are deposited by the female, possibly with the help of the long rostrum in the tissues of the ovule in the micropylar region. The grubs live at the expense of the endosperm. The adult emerges within a few days of the disintegration of the cone through an opening in the side of the testa. The adult can live for three months without food and only a limited supply of air, but where or how this period is spent is uncertain. When the male cones are ripe the insects appear in large numbers, feed on the pollen for some days, and pair. The females then visit the ovulate cones and once more deposit the eggs.

The whole life-history appears so dependent on *Encephalartos* that it would be only reasonable to find that the Cycad had demanded a *quid pro quo* and had turned the visits to use.

While it is fairly easy to understand how both colour and odour attract these insects to the male cones it is more difficult to give an explanation of how they find their way to the female, but not more difficult than in the case of numerous other insects which seek out with unerring accuracy the plants which will afford the proper food for their larvæ.

Summary and Conclusion.

E. Altensteinii grows in wooded areas, but chiefly on the more exposed cliffs.

Its height enables it often to lift its cones above the surrounding vegetation and expose them to the action of the wind.

At the time of coning the leaves are depressed, fully exposing the cones.

No visible separation of the macrosporophylls has been observed, but as certain insects effect an entrance, wind-borne pollen might also do so. Ovules are fertilised almost equally on all sides.

The male cone is fairly conspicuous and emits a perceptible odour.

Insects, viz., weevils of the genus *Phlaëphagus*, visit the male cones and thereafter, while pollen is still adhering to their bodies, the females visit the ovulate cones most probably to ovipost.

It would appear, therefore, that while nothing in the structure or position of the cones renders anemophily impossible or even improbable, entomophily is of common occurrence.

ENCEPHALARTOS VILLOSUS, Lehm.

This species, which appears to reach its western limit somewhere near the Keiskama River, is confined to the macrophyllous woods and forests of the littoral belt. Of the eight South African species of *Encephalartos* which I have seen growing in their natural habitats, it is the only one which is distinctly a shade-loving plant. When brought from the forest and subjected to the greater insolation of the open garden or park the long, graceful leaves become stunted and assume a sickly yellowish-green appearance.

Around East London it is very abundant in the wooded ravines and forest belts which fringe the lower reaches of our larger rivers. Although the character and composition of these woods are by no means uniform, they are for the most part extremely dense save where man has entered with his pruning axe. Recently the main road which passes through part of the Fort Grey forest has been widened by clearing away the vegetation on both sides, and it is almost impossible to conceive a more impenetrable barrier than that presented by the margin of the standing forest, yet in the stillness and gloom of this area *E. villosus* may be found in abundance in all stages of growth and development—indicating that neither wind nor direct sunlight are indispensable to its propagation.

Subdividing the accessory vegetation of a forest flora into "underwood" and "herbaceous undergrowth," our species may be regarded as belonging to the latter in so far as it produces no aerial stem, and the organs of reproduction seldom attain a height of more than 2 feet above the level of the soil.

Almost without exception the other plants associated with it whose flowers attain approximately the same height, are markedly entomophilous. Of these by far the most abundant in the locality mentioned are species of *Acanthaceæ* and *Labiataë*, belonging to the genera *Isoglossa* and *Justicia* in the one case and *Salvia* and *Plectranthus* in the other.

The frequency with which cones are produced under natural conditions has not yet been determined. None were observed during the period 1904–1906. In 1907 they were produced in considerable abundance in the Gonubie, Nahoon, and Buffalo valleys. Plants which I marked as coning in that year have up to the present (1912) not again developed

cones, and indeed during these years I have only found an odd cone. In cultivation both male and female specimens produce cones almost every year. The cones emerge about the same time as those of *E. Allensteinii*, namely, the end of December, but the male cones appear to take a little longer to mature, the average date being about the first week of May.

The ripe male cone reaches a height of about 24–30 inches, and is of a conspicuous yellow colour. The sporophylls which in the immature cone imbricate descendingly separate widely. It is remarkable that in *E. villosus* the microsporophyll has become more highly differentiated than in any other *Encephalartos* with which I am acquainted, and the number of sporangia is considerably below the average of the genus. Chamberlain, quoting Miss F. G. Smith, gives the number as 500, but I have never found as many as 300, and would put the average down at about 275.

Pollen is, however, produced in abundance. The upper surface of each sporophyll is slightly concave and serves to collect the pollen from the sporophylls immediately above it.

It is suggestive of the inefficiency of the wind to disseminate the pollen of this species, and that one may visit a male cone day after day during the time the sporangia are dehiscing and find it laden with pollen, whereas in a wind-swept cone, such as even that of *Stangeria*, it is only after a period of great calmness that one sees an appreciable quantity of pollen on the cone.

As Professor Pearson pointed out some years ago, the mature male cone of *E. villosus* emits a most powerful and penetrating odour, which has been said to suggest a badly kept stable. It is no exaggeration to say that by an insect with no keener olfactory sense than our own the quarry may be scented from afar, nor is it an uncommon thing for the amateur gardener to bury with indecent haste what was an object of admiration a few weeks earlier. The first male cone I carefully observed grew in the garden of a friend. We watched and recorded its progress from week to week, but there came a day when I received a polite but firm request "to remove the disgusting thing if you have any further interest in it, as not only my family but my neighbours are beginning to complain." The odour is much stronger about sunset and in dull, cloudy weather than in sunlight.

Miss Pegler first noted that this odour served to attract a species of curculionid beetle of the genus *Phlæophagus*. Her observations were recorded by Pearson (*loc. cit.*), and form the most important link in regard to the evidence for the pollination of this species. I found the same beetle in vast numbers on two male cones of *E. villosus* in 1907, and in one of them which I brought home and kept under close observation I noted that two days later the weevils were pairing. As the life-history of these insects seems so interwoven with that of *Encephalartos* it may be

worth recording that pairing occurs on the ♂ cones in the case of another weevil which frequents *E. Friderici Guilielmi*.

The female cone at the time of pollination has an average height of about 17 inches. [It has to be remembered that *E. villosus* forms no aerial stem, and that these figures therefore represent the height above the level of the ground.] The original green of the sporophylls has begun to fade into yellow, but has not yet attained the beautiful orange colour of the mature cone. As in the male, the sporophylls imbricate descendingly, and there is little or no separation at the time the microsporangia are dehiscing. It is therefore apparent that pollen settling down out of the air cannot find admission between the macrosporophylls. It is almost equally impossible to conceive how pollen borne horizontally could effect an entrance, and if it did one would expect to find only the ovules on the side of the prevailing wind fertilised. But although the results obtained by Professor Pearson and myself, after orienting the cones and examining every seed, showed that the fertilisation had occurred approximately equally on all sides, and in at least one of the cones examined I am quite certain that on two sides there were no male cones within a distance of several miles. From the nature of the imbrication only pollen carried by wind moving at an angle of at least 45° to the horizontal could possibly effect an entrance, and even then there is the difficulty of conceiving how it could reach the centrally directed micropyles. It has also to be remembered that the male cones are the taller, and that even if the wind was blowing at the required angle much the greater part of the pollen would be carried over the top of the average female cone.

An examination of almost any female cone from June onward reveals the fact that a proportion of the seeds, which may vary from 30 to 100 per cent. are parasitised by the same species of *Phlæophagus* as frequents the male cone. With the exception of two dead weevils which I found in June, 1907, with the rostrum embedded in the tissue of the ovules, and to one of which pollen masses were still adhering, I have never found the pollen-laden insects on female cones in the wild state, but in a specimen growing under almost natural conditions in our local park they were noticed in large numbers, and from the frequency with which the ovules are parasitised there can be no reasonable doubt but that the phenomenon is of regular occurrence.

Since the lower swollen peltate part of each sporophyll overlaps part of the two immediately below it, and as these curve inwardly where they meet, there is left at the time of pollination an opening large enough for a flattened insect of the *Phlæophagus* type to effect an easy entrance. The whole structure of the female cone of *E. villosus* and of one or two related species—also non-arborescent forms—differs in so many respects from the prevailing type seen in *E. Caffer*, *E. Lehmanni*, *E. latifrons*,

and *E. Altensteinii*, &c., that one is almost forced to conclude that it has either retained or evolved a disposition of its parts suited to another method of pollination.

Summary and Conclusion.

E. villosus grows exclusively in the shade of macrophyllous woods and forests.

In many places where it flourishes the force of the wind must be reduced to a minimum.

Associated plants of the same height are almost without exception entomophilous.

The male cone is of a conspicuous colour and emits a powerful odour.

Curculionid beetles are attracted to the male cones.

The same species of insect visit the female cones to deposit their eggs in the ovules immediately after leaving the male cones and while pollen is still adhering to their bodies.

The descending imbrication of the female cone makes the admission of wind-borne pollen almost impossible.

E. villosus is entomophilous.

STANGERIA.

The species of *Stangeria* to which the following observations refer is that commonly known as *Stangeria Katzeri*, described and figured by Regel in *Gartenflora*, 1874.

In the neighbourhood of East London and from there to its western limit—the Kowie River—it is essentially a *grassland* or *savannah* plant, most abundant on grassy slopes with an east to south aspect. Although it seems to hug the forest fringe it rarely enters the woods or bush-covered valleys, and when it does seldom penetrates for more than a few yards.

It is by no means a rare plant, but its distribution is curiously interrupted; for the most part it is found in groups or colonies, which are separated from one another by well-marked but variable intervals.

In any one year the *Stangerias* of a particular colony may produce cones in abundance, while in neighbouring colonies cones are either extremely rare or altogether absent.

The cones make their appearance much later than those of the local species of *Encephalartos*, being rarely visible before the latter half of April. Male cones are produced much more abundantly than females, although the proportion varies from 14:1 to 5:3.

The mature male cone reaches a height of about 12 inches, including a peduncle of 4 inches, but the actual length depends to some extent on the surroundings. Where, from the grazing of herbivorous animals or from other causes, the grass is short, the total height may not exceed

7 inches, while, on the other hand, if the grass is long or the plant, as is frequently the case, is growing in a "Kommetje," the cones may reach a height of 15 inches. These figures indicate that an attempt is made to lift the cone above its surroundings, and thus expose it to some extent to the action of the wind.

The colour of the ripe male cone varies considerably. The sporophylls are covered externally by a coat of short matted tomentum of a brown or greyish-white colour. If, however, the cone has been exposed during its growth to the action of wind and rain, the tomentum gradually disappears, revealing the chlorophyll green of the underlying tissues. A slight but distinct odour is emitted while the pollen is being shed. It is difficult and possibly valueless to attempt to estimate the intensity of an odour, but I may say that it is not sufficiently powerful to affect my own olfactory nerves at a distance of more than about 2 feet. No insects have been observed to visit the cones, except the *Lepidopter zerenopsis*, sp., which deposits its eggs freely on all parts of the plant and the neighbouring grasses. The caterpillars of this insect are very destructive of all our local Cycads, but the eggs are deposited almost throughout the year and without any reference to the production of cones.

By the end of July (24th) * the sporophylls of the more vigorous male cones begin to show signs of separating; the process advances from the base upwards with extreme slowness. At the end of August (31st) those of the apical third are still tightly closed, and it is a fortnight later (September 14th) before they show signs of separating at the summit.

Before this however (17th), the peripheral microsporangia of the lower sporophylls have turned brown and discharged their pollen.

In all it takes from five to eight weeks for a single cone to discharge its pollen, and, allowing for variations in the time of ripening of cones, pollination may be effected any time during a period of ten weeks. It is not without significance that in this neighbourhood August and September are the windiest months of the year. Moreover, in June, July, August, and the first half of September there is little rainfall, and the vegetation of the grassland is at its lowest. The grasses are dry and shrivelled, and in many parts cropped short by cattle. At no other time of the year would a plant of the dimensions of *Stangeria* have so favourable an opportunity of disseminating its pollen by the agency of wind.

On the 21st of September I kept four male cones under observation for about half an hour each. A strong westerly wind had sprung up, and its violence was great enough to cause the cones to sway from side to side and sweep out the pollen in clouds, which could be followed for a short distance moving in an upward direction. I exposed a number of micro-

* The dates refer to the most vigorous specimen of one of 13 cones kept under continuous observation from the 13th of July to October, 1912.

scopic slides smeared with glycerine for about an hour at distances varying from 3 feet to ten paces from male cones, and in every case was successful in finding pollen grains, most being caught by a slide exposed on the top of an ant-heap about $3\frac{1}{4}$ feet high.

The distances from male cones are not great, but in the area where these observations were made male cones were growing 8 inches, 26 inches, 37 inches, and 54 inches from females, and it is thus clear that wind is able to convey the pollen of *Stangeria* sufficiently far to insure the pollination of a fair number of cones. The fact that most pollen was found on the slide exposed on an ant-heap would indicate that the pollen is carried well up into the air, and is therefore capable of being disseminated over a wide area.

At the time of the pollination the ovulate cones are from 5 to 7 inches high, and have a circumference of $7\frac{1}{4}$ inches. In all ordinary circumstances, and except where the surrounding grass has grown very rank, these dimensions are sufficiently great to insure an open way from above if not from the sides. The macrosporophylls are much larger and fewer in number than the microsporophylls, and are arranged in a series of six (rarely five or seven) vertical rows with ascending imbrication. In contrast to what has been observed in the case of *Encephalartos*, the macrosporophylls separate and open out at the time of pollination, the openings pointing upwards. The lower sporophylls in some cones open out considerably more than the upper. The whole arrangement seems adapted to catch pollen settling down out of the air rather than borne horizontally by wind currents. A careful study of the female cone at this stage will show that the pollen which falls on the smooth adaxial surface of any one sporophyll has much less chance of reaching the ovules of that sporophyll than it has of coming in contact with those which form the right and left of the two sporophylls immediately below it.

The sporophylls remain open for five or six weeks. No insects have been observed to visit the female cone, and none have been found in the seeds at any stage of their development. In some years a fair number of cones set seeds, and these are evenly distributed throughout the cone. I have records of only two cones in which the fertile seeds were confined to one side of the cone. One was found growing slantwise out of a hollow and in such a position that pollen, whether settling down from above or driven sidewise, could only reach one side. Unfortunately I did not see the cone until it was almost disintegrating, and cannot be perfectly certain that it occupied the same position at the time of pollination, although I have no reason for believing that it did not. The other was growing inside the bush on the slope of the east bank of the Nahoon, and was the specimen which had penetrated furthest into the woodland formation. Wind-borne pollen could only have reached it from the side on which the fertile seeds were found.

The comparatively long period—about nine months—which elapses between pollination and the maturing of the seeds, exposes the cones to many risks, so that it is difficult from mere field observations to estimate the frequency of pollination; but after allowing for the heavy toll levied by grass-fires, caterpillars, and the trampling of oxen, one is left with the impression that the production of seeds is not a very successful business. This impression is confirmed by the apparent rarity of seedlings, but again it has to be remembered that in a grass country it would need very careful and minute observation to pick out small plants, and consequently they may be commoner than one thinks.

This year I have labelled most of the female cones in a *Stangeria* colony, and hope to get more accurate data on this point.

In any case *Stangeria Katzeri* has very successfully adopted vegetative means of reproduction. Branches and suckers up to a dozen in number are found in almost every well-developed specimen.

Summary and Conclusion.

St. Katzeri grows in open grassland or savannah.

The male cones shed their pollen from the middle of August onward, when the grass is dry and shrivelled and high winds are common.

The male cones are sufficiently high to enable the wind to sweep out the pollen.

The sporophylls of the cones imbricate ascendingly; those of the female cone separate at the time of pollination. This arrangement is well adapted to catch pollen settling down from above.

Pollen has been caught on slides placed at distances which were greater than those separating several male and female cones.

No insect visitors which could effect pollination have been observed.

Pollination takes place in a fair number of cases, but does not appear to be of general occurrence.

Vegetative reproduction is common, and may have been adopted to supplement the more uncertain sexual method.

Anemophily holds good for *Stangeria Katzeri*.

The three species of Cycads considered in the present paper may be found in certain localities within a radius of a hundred yards—*Stangeria* in the grassland abutting sharply on the bush-covered valleys, *E. Altensteinii* on the steeper banks of the valley, and *E. villosus* in the shady depths of the valley itself; yet if my conclusions are correct they represent three stages or conditions in respect of their pollination.

Stangeria adheres to what we may assume to be the older and more primitive anemophilous method, and it is not without significance that

there is much in its general habit and structure to suggest that it is nearer the ancestral stock morphologically than *Encephalartos*, e.g., in its low fern-like habit, its leaf structure, its less differentiated sporophylls, its tendency towards a concentric structure of the cotyledonary bundles.

E. villosus, on the other hand, appears to have abandoned anemophily completely and to rely entirely on insect agency. There is no denying that the method is an expensive one, although not more so than in many other species of plants; but certainly, if one may judge from the number of young plants seen, it has proved successful. There are indications that owing to the greater certainty of entomophily *E. villosus* has been able to economise in several directions—if one may put the matter so unscientifically. There is no need to lift its cones on a long, slowly developed stem in order to bring them into a position favourable to the action of the wind, which its habitat would demand. As a consequence the age of cone production is probably reached much earlier—a point confirmed by the comparative growth of young plants of this and other species. There is also evidence that a considerable reduction both in the number of microsporophylls and sporangia has taken place. Complete records have not yet been obtained, but the number of both these organs is certainly much smaller than in such forms as *E. latifrons* and *E. Friderici Guilielmi*, both of which grow in open grassland.

Without access to the literature of the Cycadaceæ it is impossible to say to what extent the arrangement of the sporophylls with downward imbrication prevails in the family, and therefore to what extent it indicates an entomophilous condition. It is at least interesting that our three species differ so markedly in a feature of this nature, which must of necessity be closely related to their pollination.

E. Altensteinii appears to represent an intermediate condition wherein both forms of pollination are possible. In the colouring of the staminate cone, in the odour emitted by it, and in the arrangement of the sporophylls it stands almost midway between *Stangeria* and *E. villosus*. Have insects of the *Phlæophagus* type more recently extended their operations to *E. Altensteinii* than *E. villosus*? If this question could be answered in the affirmative, would it not help us to understand how this species is being fitted to leave the open wind-swept krantz for the shelter of the wooded kloof?

Most of the points have been discussed with Professor Pearson of the South African College, and I would like to take this opportunity of acknowledging that the observations were begun under his inspiration and continued with his unwearying advice and assistance.